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A contribution to the question of the distribution and evolution of plecopterological communities in Europe

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Hitherto research work dealing with Plecoptera in the major part of Europe has shown of what importance this component of the bottom fauna is for getting to know the biocenose of running waters. The study of stoneflies is of much greater importance than has been assumed till now. From the theoretical point of view it contributes a significant share to the solution of numerous biogeographical problems, while from the practical point of view Plecoptera are an important indicator of the quality of waters. At present the question of sufficiency and purity of water is a world-wide problem and the relevant agencies of the United Nations Organisation are occupying themselves with the use of water sources today.

The synecological aspect of plecopterological communities is of greater importance than the autecological one, even though it is clear that in the system of correlations within the biocenose Plecoptera do not form a self-contained association unit. They are only an integral part of one unit, closely associated with the conditions and the factors of the environment. Thus 'Möbius' biocenose is, in essence, actually Sukachev's geobiocenose or Tansley's eco-system.

As long as we shall speak of plecopterological associations we understand under the term "association" group of individuals of a certain relict insect order participating often very significantly in the structure of the entire hydrobiocenose.

At the last Symposium in Plön (1964) I tried to show on the example of the evolution of Czechoslovak plecopterological associations (Raušer 1964) what points of view we can take into consideration in their delimitation in the landscape. The present state of the study of Plecoptera in Europe permits already today to shape their association classification everywhere where quality data and records are available. From some countries we are still lacking reports and more detailed studies, on the one hand, from the area of the Russian platform, on the other hand, from the northern regions of East Europe. The Balkan peninsula, too, is little known to date. On the other hand, the classical works of Brinck (1949), Hynes (1941), and Illies (1952), who found their younger successors mainly in Western Europe (Berthélemy 1964), are already available today.

The European plecopterological association have not yet been systematically studied. From the plecopterological point of view, Illies' Limnofauna Europaea (1967), which we can consider to be basic compendium furnishing a clear picture of the present distribution of species, is available. At the same time the distribution forms the basis for the correct understanding of the geohistorical evolution of plecopterological associations in the youngest geological (Quaternary) period. On its basis we can then tackle the answer to historico-zoogeographical questions with the aid of paleoclimatic and paleogeomorphological knowledge.

Methods

In the treatment of plecopterological associations in Europe two inseparable components of the eco-system have been taken into account: species composition and water type. The first component was the subject of Brinck's (1949), the second one of Hynes' (1941) classifications. For a smaller territory like Czechoslovakia I used the simplified Brinck's system, which, compared with the original 5-stage one, was a 4-stage one. Accordingly, the scale for small territories has the following tiers:

0 = both species *do not occur* in the same water type together
1 = both species are common to one or more water types; however, they do not appear in the same locality in a maximum number
2 = both species occur most numerously in the same locality; but both are also present in the other water types as well
3 = both species occur only in a certain water type; only exceptionally and qûite isolatedly do they appear also in other water types.

As our conclusions have shown it is suitable not only for the small territory of Central, but also of South Europe (Balkan peninsula).

We can quote an example from the Czechoslovak territory (The Morava River basin). Together 965 localities have been investigated, belonging to 6 water types. Let us compare the correlations of three species:

A *(Capnia bifrons)*, B *(Leuctra teriolensis)* and C *(Leuctra fusca)*:

Water type / Species	I	II	III	IV	V	VI
A	1	128	72	12	3	0
B	0	0	0	24	15	96
C	65	195	84	92	12	2

According to the above mentioned scale the generic combination in the first water type is as follows: A : B = 0, A : C = 1, B : C = 0, in the second type A : B = 0, A : C = 2 etc.

For large-area units this detailed classification system is not suited for the reason that numerous complexes of species belonging to groups O and 1 are atypical both for the association and for the water type. For the characteristic of European associations and for the biological typisation of watercourses I consider the last two tiers to be most characteristic. Particularly typical are the species combinations of the third group.

Let us quote an example, also from the Czechoslovak territory. In the three water types of Central Europe (the lenitic type, the hilly-land type and the mountainous type) together 50 species have been established (to compare the association diagrams No. 9, 16 and 22) from which in the species: A *(Protonemura autumnalis)*, B *(Leuctra hippopus)*, C *(Leuctra handlirschi)* and D *(Isoperla oxylepis)* the following correlations could be observed:

Water type / Species	I	II	III
A	0	80	138
B	2	214	116
C	0	59	396
D	0	935	27

It follows from the number of the found specimens that in the Ist (= lenitic) water type there exist the following correlations: A : B = 0, A : C = 0, A : D = 0, B : C = 0, B : D = 0; in the IInd type: A : B = 3, A : C = 2, A : D = 2, B : C = 1, B : D = 2, C : D = 1; in the IIIrd type: A : B = 2, A : C = 3, A : D = 1, B : C = 3, B : D = 2, C : D = 2 etc. From these correlations the groups 2 and 3 have been taken into consideration in the diagrams.

From the hydrological point of view we can differentiate in Europe on the whole three types:

the lenitic (slowly running), the hilly-land and piedmont type and the mountain type. All these types differ from one another not only physically, but also by their chemical properties, irrespective of the acidophilous or alkaliphilous character of the substratum which naturally still increases the differences in their chemism.

The lenitic tier includes streams with a very low fall partly in the lowlands, partly in the uplands with considerable temperature variations, differently long lasting frosty weather according to the latitude and a markedly varying oxygen content. In the character of the bottom sediments, sand and mud prevail.

The hilly-land and piedmont tier is the prevailing type of European streams in general. The temperature variations are lower and the frosty weather, as a rule, lasts for a shorter period than in the preceding tier. In the character of the bottom, stones, gravel and in places also sand prevail.

The mountainous tier contains, in essence, two types: streams and lakes. Both differ greatly in physical and chemical respects. The first type features temperatures greatly balanced through the whole year, while frosty weather even in relation to the low temperatures lasts for a relatively short time. The bottom is covered with boulders and stones.

According to this classification, association diagrams have been plotted. In each diagram the differential species (T) have been represented. The individual generic combinations have been arranged so that first the most numerous species and than the less numerous species have been quoted. The associations have been given their name according to characteristic generic combinations.

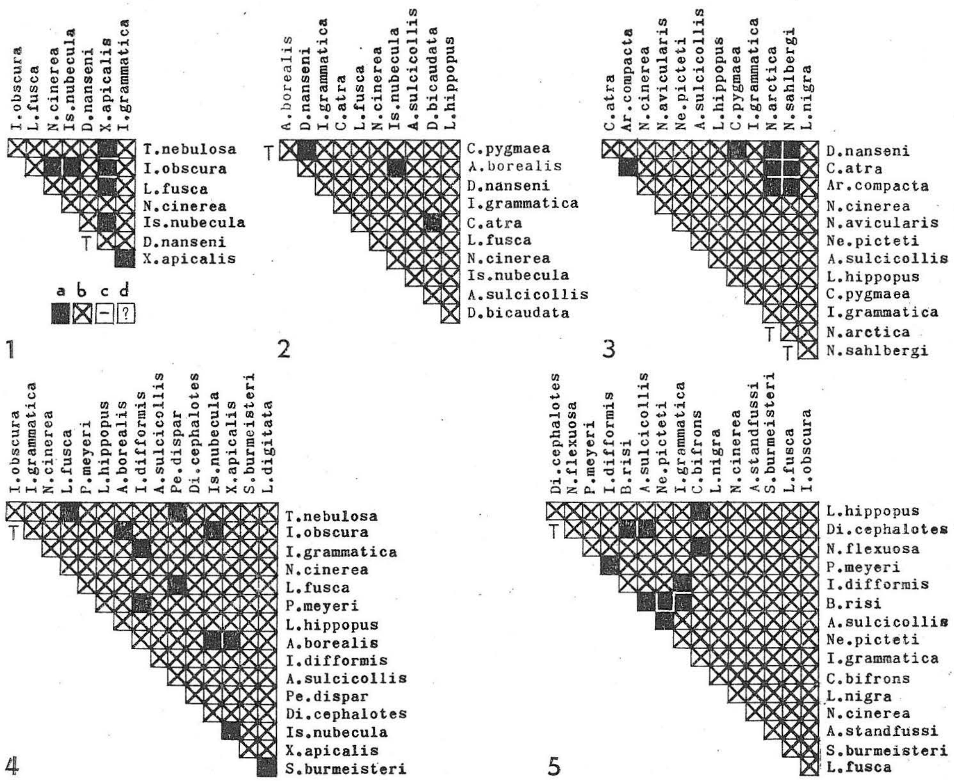
Each association is divided further into so-called variants (subassociations). According to the hydrological and coenological system, it follows that the European associations of Plecoptera can be zonally divided into 4 zones: arctic, boreal, temperate and Mediterranean. With the exception of the arctic zone, three tiers can be determined in the other zones: lenitic, hilly-land and piedmont, and mountainous.

For the determination of the Plecoptera associations in Europe considerable comprehensive material from a total of 34,128 localities plus the simultaneous knowledge of 345 species from 34 European genera has been used. The actual research work was performed in the territories of Czechoslovakia, Bulgaria, and Yougoslavia, while in the other cases we relied on the results of European plecopterologists. Their often very valuable data have been a guide for me in the elaboration of the association groups. The occurrence of species combinations in various types of European rivers and streams haven been studied and statistically evaluated, their classification being carried out accordingly.

At the same time it is necessary to remark that, e.g. the Swedish lenitic watercourses correspond rather to the hilly-land ones in Central Europe and the higher situated streams of the European Mediterranean. These inherent laws were already stressed by botanists (Brockmann-Jerosch 1913) and they appear to hold good also in zoogeography. When giving names to plecopterological associations, Braun-Blanquet's system (1951) was used as a model.

The association as the basic phytocenological unit of the Zürich-Montpellier system naturally cannot be compared with the plecopterological communities. Likewise the hierarchy of the geobotanical system cannot, for the time being, be used for the sociological classification of Plecoptera. That is why we use the term "Association" as a general word for communities of any taxonomical quality. For designating associations we availed ourselves of a combination of true species (Kennartenkombination), for the individual variants, in turn, differential species (Trennart).

Accordingly, we can divide the communities of Plecoptera in Europe into the following zones and tiers:



Arctic zone. Fig. 1. As. (=Association) of the lenitic currents. Fig. 2. As. of the hilly-land and piedmont currents. Fig. 3. As. of the mountain currents and lakes. Boreal zone. Fig. 4. As. of the lenitic currents. Fig. 5. As. of the hilly-land and piedmont currents.

Explanations: a = combination of species, which occur only in a certain water type; only exceptionally and quite isolatedly do they appear also in other water type, b = combination of species, which occur most numerously in the same locality; but both are also present in the other wather type, d = occurrence of the species combination problematic. T = differential species.

I Survey of European Plecoptera Associations

Arctic zone

This zone occupies in Europe an insignificant area beyond the northern timber-line which coincides with the approximately 10^0 isotherm of the warmest month (= type of snow climate according to W. Köppen). It is characterized by tundra with permanently frozen ground close under the surface, with small rivers and streams and stagnant water in the plains, hilly-land and mountainous regions.

A. Lenitic currents

These streams are found in territories about which we practically do not have any newer and more accurate data (Kanin peninsula, Malozemelskaya and Bolshezemelskaya tundras). According to Brinck's investigations 1949) in the north of Sweden and that of Meinander (1967) in northern Finland there exists here a single association, namely

as. *Taeniopteryx nebulosa — Isoperla obscura* (Fig. 1)

with species that are close for their correlations to the lenitic currents of the boreal zone and have a wide distribution. With the exception of the arctic and circumboreal species *Diura nanseni,* the other species are distributed all over Europe. Involved are taxons giving preference to streams with a higher discharge (over 6 cu. m/sec). Yet, they do not avoid smaller currents. The differential species of this association is *Diura nanseni.*

B. Hilly-land and piedmont currents

These streams of the arctic zone are found mainly in the north of the Scandinavian peninsula. Their plecopterological populations were studied by Brinck (1949), so that according to this precise results we can also determine the association characteristic for this water type.

As. *Capnia pygmaea — Amphinemura borealis* (Fig. 2)

Both true species give the general character of the association in which both species of the previous tier (*Diura nanseni, Leuctra fusca, Nemoura cinerea,* etc.) and species common to mountain currents (*Amphinemura sulcicollis, Leuctra hippopus,* etc.) occur, besides species specific of the association (*Capnia atra*). In the general character of the association, the species with a wide distribution (*Leuctra fusca, Isogenus nubecula*) prevail again, while others reach as far as the southern border of maximum continental glaciation (*Capnia atra*).

C. Mountain currents and lakes

They include the Swedish and Norwegian "jokks", the North Scandinavian mountain lakes and the lakes of the Polar Urals. The specific conditions of the environment (cf. Brinck 1949 : 202—207) are reflected also in the structure of the association which belongs to

as. *Capnia atra* — *Diura nanseni* (Fig. 3)

In the community are dominant, besides both true species, *Arcynopteryx compacta, Diura bicaudata,* euryoecic *Nemoura cinerea,* and others. Some species, such as *Nemoura avicularis, Nemurella picteti,* occur, as a matter of fact in the preceding water types, but they are not found in large numbers in the same locality, or are not common to a certain water type alone. This applies also to the species *Diura nanseni* which occurs in very large numbers in the jokks (120 individuals in 13 currents), but in the mountain lakes it is quantitatively much less represented (15 individuals in 5 lakes). As outstanding differential species for the jokks we can denote *Nemoura arctica* and probably also the rare *Nemoura sahlbergi.*

Boreal zone

This zone is approximately identical with the region of the boreal coniferous forest (= boreal type according to W. Köppen). The equatorial boundary is formed approximately by the -3^0 isotherm of the coldest month, while the 10 ^{0}C isotherm of the hottest month forms the polar boundary. The entire area of the territory is marked by a longer lasting snow cover, mostly by a short summer and high water levels in the spring months and the beginning of summer (nival mountainous type according to M. Pardé). Rain and ground waters form a less substantial component of the runoff. With it is also connected the temperature balance of the water which reflects itself in the synusia of the benthonic fauna. This zone occupies almost the entire Scandinavian peninsula and the north of the Russian platform. We can distinguish three tiers.

A. Lenitic currents

These streams occupy a considerable area of Fennoscandia and the entire territory of the Russian platform in the area of the boreal zone. Brinck's work (1949) informs us about the character of the plecopterological populations. The lenitic currents are populated by

as. *Taeniopteryx nebulosa — Isoperla obscura* (Fig. 4)

This community is characterized by the progressive species of the lowland streams in which all species occur in this type also in the temperate zone. Involved are taxons that after the regression of the Pleistocene glacier populated this territory. A considerable part is formed of the euryoecic species (*Nemoura cinerea, Leuctra fusca, Isoperla obscura,* etc.). Some of them belong to the community of the Central European hilly-land and piedmont currents (*Leuctra hippopus*).

B. Hilly-land and piedmont currents

These streams are encountered especially on the eastern, gentle slops of the Scandinavian peninsula. In the populations there are again present numerous species of the Central European hilly-lands (*Brachyptera risi, Amphinemura sulcicollis, Nemoura flexuosa,* etc.), besides the species of the Central European lowland streams and peneplains (*Isoperla difformis*). For the different types of currents the basic

as. *Leuctra hippopus — Dinocras cephalotes* (Fig. 5)

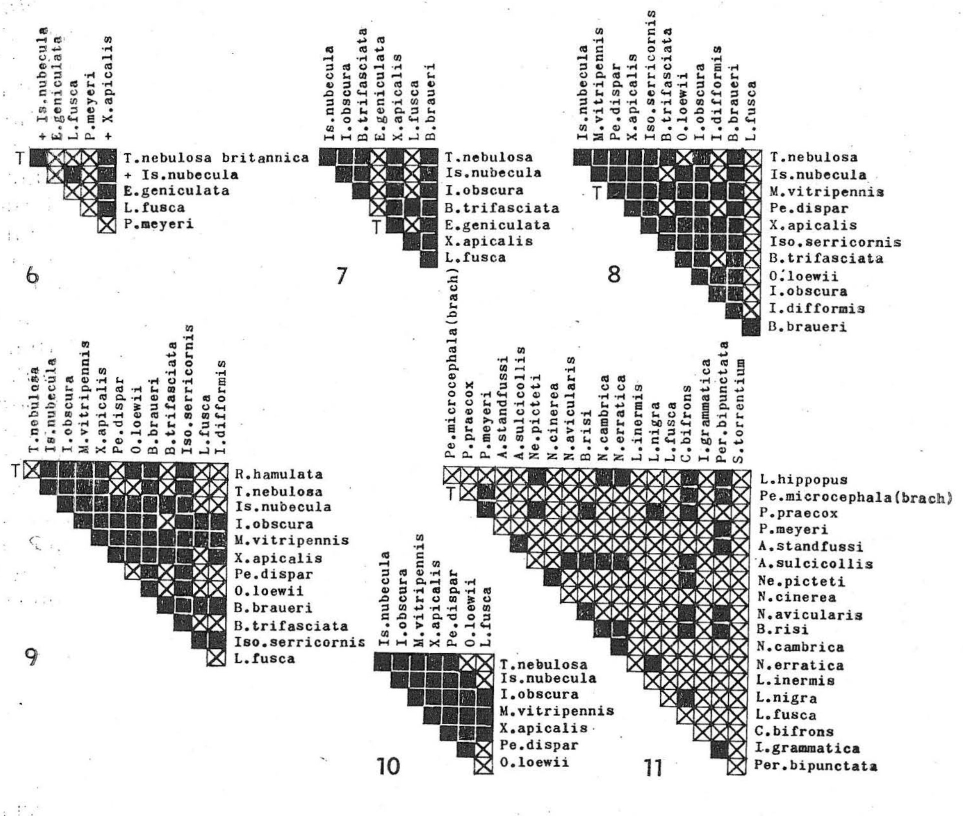
is common, which includes species amply distributed also in Central Europe with the exception of *Siphonoperla burmeisteri* with an interesting area in Scandinavia.

C. Mountain currents and lakes

They lie in the climatic tier of the nival climate and in respect of vegetation are characteristic for their mountain tundra. They are populated by species of the as. *Capnia atra — Diura nanseni* as has already been said (see page 38).

Temperate zone

This zone is richest in species, which reflects itself also in the number of plecopterological associations and variants. Climatically it is not homogeneous, which manifests itself also in the water types. The entire territory, originally covered with deciduous and mixed forests belongs to the beech climate (according to W. Köppen) and can be divided roughly into three units: western, central, and eastern. Connected with it are also the regionally specific conditions in the regime of watercourses which reflect themselves in the plecopterological associations.



Temperate zone. L e n i t i c   c u r r e n t s. As. *Taeniopteryx nebulosa — Isogenus nubecula.* Fig. 6. Var. (=Variation) insular with *Taeniopteryx nebulosa britannica.* Fig. 7. Var. West European without *Marthamea vitripennis.* Fig. 8. Var. Central German with *Marthamea vitripennis.* Fig. 9. Var. Pannonian with *Rhabdiopteryx hamulata.* Fig. 10. Var. Eastern without *Brachyptera trifasciata.* H i l l y - l a n d   a n d   p i e d m o n t   c u r r e n t s. Fig. 11. As. insular *Leuctra hippopus — Perlodes microcephala.*

A. Lenitic currents

These streams have the same basic association as the currents of this type in the boreal zone. In them are found

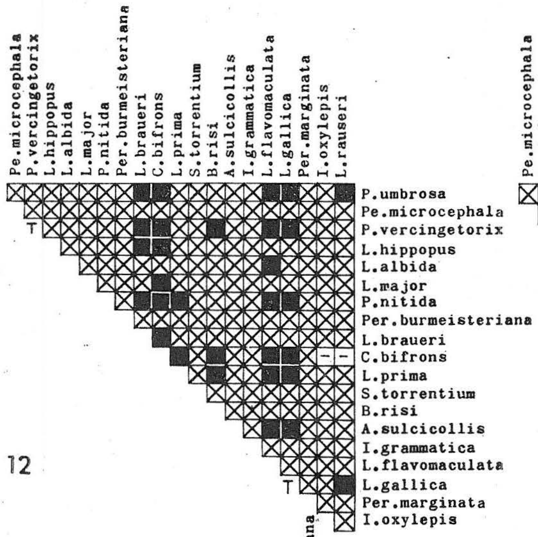
as. *Taeniopteryx nebulosa — Isogenus nubecula*

totalling five, insignificantly different variants. For the British Isles is typical var. insular with *Taeniopteryx nebulosa britannica* (Fig. 6) with the insular geographical race and with a poor species representation. In the community is typical the atlantic species *Euleuctra geniculata.* Of the other species, two (*Isogenus nubecula* and *Xanthoperla apicalis*) can only reconstructionally be assumed. Var. West European without *Marthamea vitripennis* (Fig. 7) is under the influence of the Atlantic climate with warmer rainy winters and autumn rains and cooler summers. A specifity of the otherwise indistinct variant is the Lower Rhenish *Marthamea selysii.* In respect of species it is more variegated than the preceding variant. Var. Central German with *Marthamea vitripennis* (Fig. 8) is in respect of species the richest and contains species penetrating in the post-Pleistocene period from the east to the west (Ost-West-Arten according to Illies 1953: *Oemopteryx loewii, Marthamea vitripennis, Isoptena serricornis*). It is distributed over the transitional climate and its western boundary is the Rhine, while in the east it extends as far as the Vistula and the Bug. Similarly as the two preceding variants it is today deprived on larger rivers of some lowland species (*Oemopteryx loewii, Isoptena serricornis, Xanthoperla apicalis*). Var. Pannonian with *Rhabdiopteryx hamulata* (Fig. 9) characterizes the lowland currents of wide flood-plains. It comprises species that are identical with the preceding variant. Some of them penetrate also to the hilly-land currents (diferential species *Rhabdiopteryx hamulata, Oemopteryx loewii, Taeniopteryx nebulosa, Perlodes dispar, Isoperla difformis*), but here they are not typical members of communities. It is typically developed in Pannonium. It contains again Ost-West-Arten as understood by Illies. Var. Eastern without *Brachyptera trifasciata* (Fig. 10) is a subassociation of the rivers and streams in the Russian platform. It is a hitherto little known community and its species composition was compiled according to Jacobson-Bianki (1905) and Zhiltzova 1964). As to composition it resembles the Central German variant where some lowland species, penetrating to the West, are missing.

B. Hilly-land and piedmont currents

These streams have very and regionally differing communities. The variety of plecopterological associations of hilly-land currents is seen in their geohistorical evolution without Pleistocene continental glaciation. In essence, we can distinguish two basic associations: British and continental. In the first the true species *Protonemura umbrosa* is replaced by the wide spread species *Leuctra hippopus.*

As. continental *Protonemura umbrosa**) — *Perlodes microcephala* is similar to the continental association. It is lacking, however, the species that did not penetrate beyond the border of maximum continental



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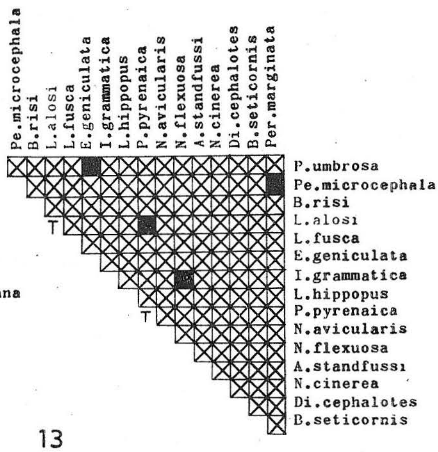

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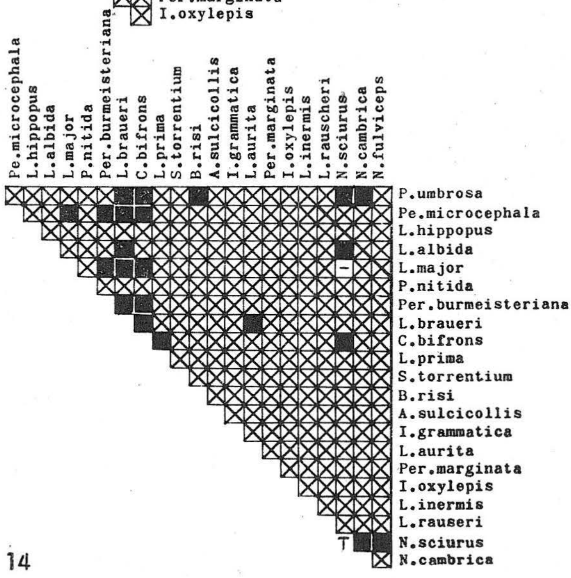


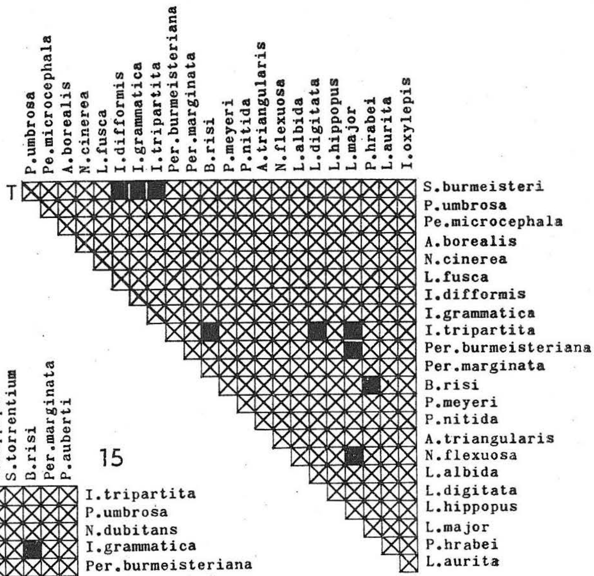
14

Temperate zone. Hilly-land and piedmont currents. As. continental *Protonemura umbrosa — Perlodes microcephala.* Fig. 12. Var. Central Massif with *Protonemura vercingetorix.* Fig. 13. Var. Subpyrenean with *Leuctra alosi.* Fig. 14. Var. Central European with *Nemoura sciurus.*

glaciation (*Leuctra albida, L. major, Protonemura umbrosa,* and others). Thus it resembles rather the Scandinavian type of as. *Leuctra hippopus — Dinocras cephalotes.* This type of community occurs in Middle England, Scotland, and Ireland.

As. continental *Protonemura umbrosa — Perlodes microcephala*

differs from the previous by presence of the Central and South European species *Protonemura umbrosa.* It comprises a total of 7 variants differing by differential species, thus being different from one another. In



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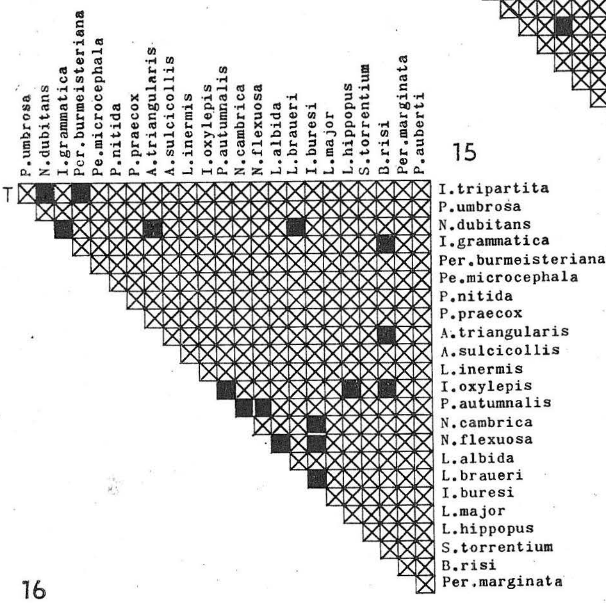

16

Temperate zone. Hilly-land and piedmont currents. As. continental *Protonemura umbrosa — Perlodes microcephala.* Fig. 15. Var. Bohemian with *Siphonoperla burmeisteri.* Fig. 16. Var. Slovakian with *Isoperla tripartita.* Fig. 17. Transylvanian with *Protonemura aestiva.* Fig. 18. Var. Stará planina with *Perla marginata bureschi.* Mountain currents. Fig. 19. As. British *Protonemura montana — Capnia vidua.*

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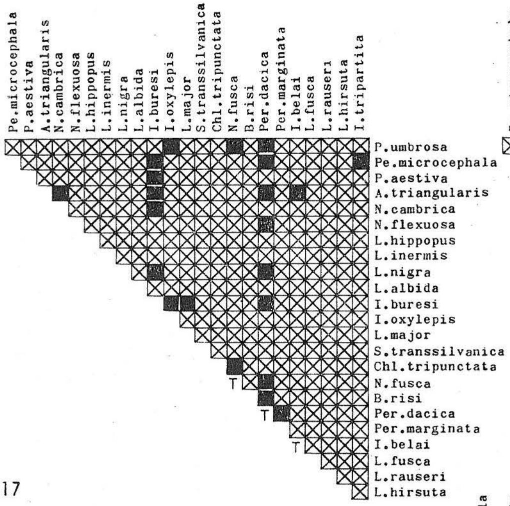
*) *Protonemura umbrosa* in the following text and in the association diagrams (Fig. 12—18, 28, 34, 38—40) is *Protonemura intricata* (Zwick i. litt.)

the sphere of the Atlantic climate is typical var. Central Massif with *Protonemura vercingetorix* (Fig. 12). Numerous species (*Leuctra hippopus, L. albida, L. major, Protonemura nitida,* etc.) are common to all the other variants, while others are typical of the streams of this type (*Protonemura vercingetorix, Leuctra flavomaculata, L. gallica,* etc.). The presence of the North Spanish species of *Leuctra lamellosa* points to the relationship with the Iberian associations.

Var. Subpyrenean with *Leuctra alosi* (Fig. 13) on the northern slopes of the Pyrenees possesses already a number of specific features of the Pyreneic mountain association (Berthélemy 1966) with the species



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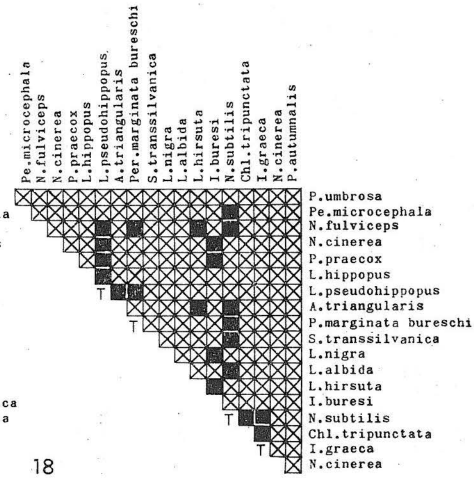

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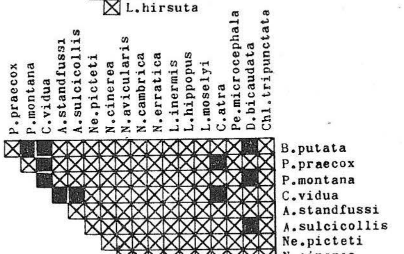


19

Protonemura pyrenaica, Pachyleuctra benlocchi, etc. The fundamental structure of the variant, however, is formed here of wide-spread species (*Brachyptera risi, Leuctra fusca*), the Central European species (*Leuctra* *aurita*), and the Central-South European ones (*Protonemura umbrosa*). Besides the differential species *Leuctra alosi,* there are also other, yet in the hilly-land association rarely occurring, species (*Pachyleuctra benlocchi* and others).

Var. Central European with *Nemoura sciurus* (Fig. 14) is wide-spread in the Hercynian uplands. An outstanding feature of this variant is the predominance of the Central European and Central-South European species over the holo-European ones. Of importance is the presence of the Central European *Leuctra braueri,* which in brooks with a sandy bottom is found in abundance. As to its composition the variant resembles the Bohemian and West-Carpathian ones.

Var. Bohemian with *Siphonoperla burmeisteri**) (Fig. 15) is restricted to the Bohemian Highlands. Involved is a well-defined variant where *Siphonoperla burmeisteri* is limited to the river basins of the Labe (Elbe) and the Vltava (Moldau). In some species of the community (*Nemoura dubitans, N. sciurus*) the abundance is greater than in the neighbouring West Carpathian one. In it we can distiguish another two tiers, characterized by a combination of the species *Perla burmeisteriana* and *Capnia bifrons* in the lower-lying regions, while in the higher-lying ones of *Brachyptera seticornis* and *Taeniopteryx hubaulti.*

Var. Slovakian with *Isoperla tripartita* (Fig. 16) covers the territory of the West Carpathian hilly-lands, on Slovakian and Polish territory up to the tectonic line of Ondava-Visloka. By the differential species of *Protonemura autumnalis, Isoperla tripartita* differs from the Hercynian variants, while, on the other hand, it is nearer to the following East Carpathian variant (*Isoperla bureši*). Again also here two tiers lying one over the other can be distinguished.

Var. Transylvanian with *Protonemura aestiva* (Fig. 17) has a whole number of endemic species (*Nemoura fusca, Isoperla belai*), which differentiate it from the West Carpathian one and are described mainly by Illies and Kis. The stock of the variant is again formed of the Central European and Central-South European species. In addition to them, also South European species (*Perla dacica*) occur.

Var. Stará planina with *Perla marginata bureschi* (Fig. 18) has rather the Central European than Balkan aspect, except for the southern slopes of Stará planina with Hellenic elements (*Amphinemura arcadia*) and endemic species (*Isoperla submontana, Leuctra pseudohippopus*) which, however, play only the role of differential species without higher frequency.

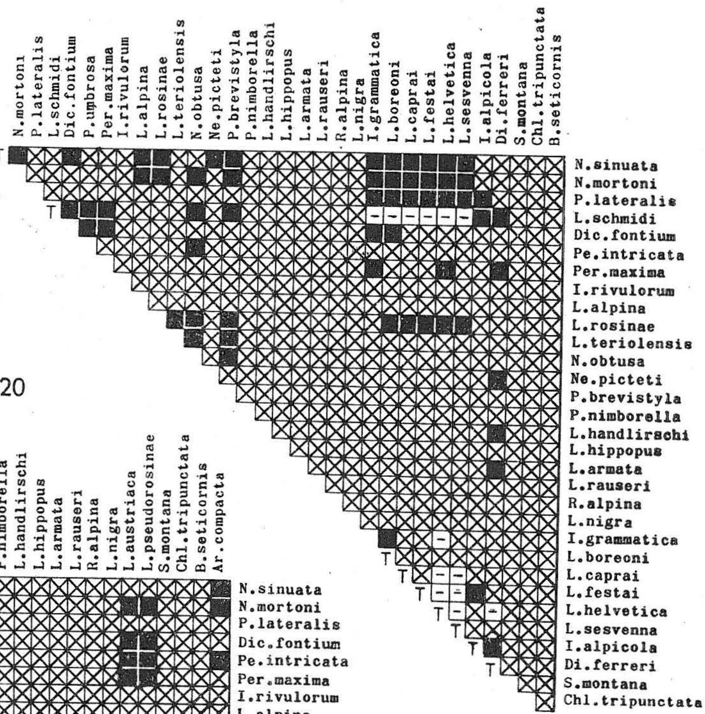
C. Mountain currents

These streams are much more variegated and feature a typical community in the various regions of the temperate zone. Their diversity follows from the species structure where besides "generic", evolutionarily older species, also younger ones are present, coming from the Würm and the Riss periods (cf. Raušer 1962). Also in this type of current, two associations can be distinguished.

*) *Siphonoperla burmeisteri* (also Fig. 15) is *Siphonoperla taurica* (Zwick i. litt.)

As. British *Protonemura montana — Capnia vidua* (Fig. 19)

developed in the mountainous regions of Great Britain. Due to Pleistocene glaciation, the continental Central European species distributed in the following association are missing here. The community has neither a specific differential species that would not be present in an other territory. The overall habitat of the association does not feature any pronounced alpine character either as the subsequent alpine variant does.



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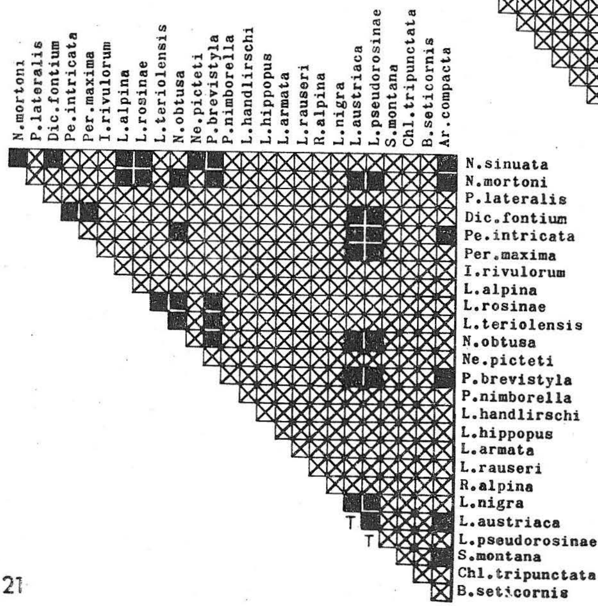
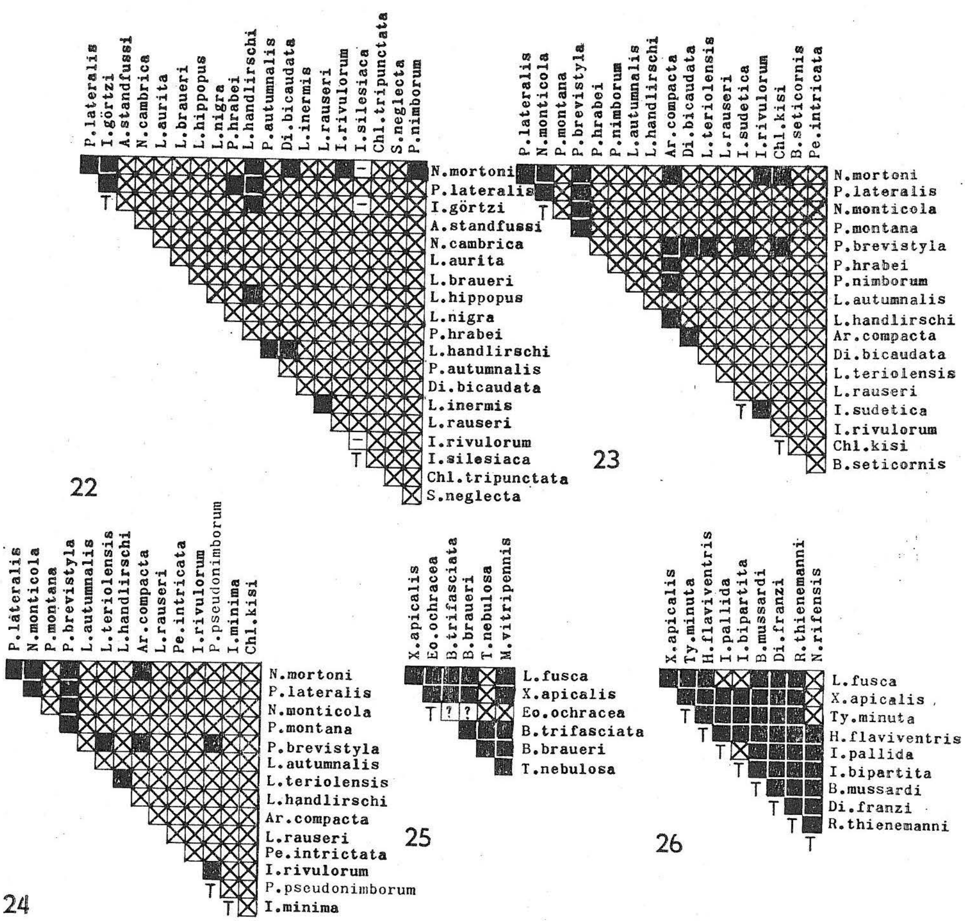


21

Temperate zone. M o u n t a i n c u r r e n t s. As. *Nemoura mortoni — Protonemura lateralis.* Var. Alpine with *Nemoura sinuata.* Fig. 20. West Alpine unit with *Leuctra schmidi.* Fig. 21. East Alpine unit with *Leuctra digitata.*

As. European *Nemoura mortoni* — *Protonemura lateralis*

is characterized by typical mountainous species of the Central European type. It can b e divided into four variants corresponding qualitatively to the length of the development of the mountain unit, quantitatively to its spaciousness. The richest variant is var. Alpine with *Nemoura sinuata,* a differential species of this mountain range. In essence, we can distinguish here two different units where genetically different differen-



Temperate zone. Mountain currents. As. *Nemoura mortoni* — *Protonemura lateralis.* Fig. 22. Var. Hercynian with *Isoperla görtzi.* Fig. 23. Var. West Carpathian with *Nemoura monticola.* Fig. 24. East Carpathian with *Protonemura pseudonimborum.* Mediterranean zone. Lenitic currents. As. *Leuctra fusca* — *Xanthoperla apicalis.* Fig. 25. Var. Iberian with *Eoperla ochracea.* Fig. 26. Var. thermophile with *Tyrrhenoleuctra minuta.*

tial species occur. However, we cannot speak of two different variants, because geographically and orographically a hard-and-fast line between the Western and Eastern units cannot be drawn as it is the case, e.g. in the Carpathians. Therefore, we talk only of West- and East Alpine units. In either unit we could further distinguish two tiers: a lower one with *Taeniopteryx kühtreiberi* and a higher with *Rhabdiopteryx alpina.*

1) West Alpine with *Leuctra schmidi* (Fig. 20) differs from the following by abundance of West Alpine endemic species (*Leuctra boreoni, L. caprai, L. festai, L. helvetica, L. sesvenna, Isoperla bipartita*). In either unit is missing Perlodid *Diura bicaudata* and *Arcynopteryx compacta* occurs only in the most eastern regions of the following unit. It is, however, necessary to stress that this unit is older in evolutionary respect — inasmuch its biota is concerned — than the eastern one.

2) East Alpine with *Leuctra digitata* (Fig. 21) has only two hitherto known endemic species (*Leuctra austriaca, L. pseudorosinae*), which is also connected with the geohistorical development of its biota (cf. Rašer 1962). Otherwise its structure and interspecies relations are the same as in the preceding unit.

Var. Hercynian with *Isoperla görtzi* (Fig. 22) occupies the Hercynian mountainous regions. The isolatedness of the individual mountain ranges often reflects itself locally rather markedly also in the character of the community. That is why we can distinguish in the regional analysis several variants (cf. Rašer 1964), such as in the mountainous regions of the Bohemian Highlands. These locally different units actually distinguish themselves by the abundance of the differential species which, however, as investigations have shown, can also occur in other, mutually isolated mountain ranges (*Isoperla silesiaca*). From the all-European point of wiev it is, therefore, more expedient to consider the community with *Isoperla görtzi* as uniform for the Hercynian mountainous regions.

Var. West Carpathian with *Nemoura monticola* (Fig. 23) has a number of species of the community common with the East Carpathian one. The alpine *Protonemura nimborella* is represented by *Protonemura montana* here. Some species typical of the Alps (*Rhabdiopteryx alpina,* the *Leuctra* species) are missing here; on the other hand, *Arcynopteryx compacta* and *Diura bicaudata* are in great abundance. For this community we can consider next to *Nemoura monticola* also *Isoperla sudetica* as differential species.

Var. East Carpathian with *Protonemura pseudonimborum* (Fig. 24) is similar to the West Carpathian (*Protonemura brevistyla*) and the Alpine ones (*Rhabdiopteryx alpina*). From the two preceding ones it again differs by the differential species (*Protonemura pseudonimborum, Isoperla minima*), specific for certain mountain units of the entire Eastern Carpathians. In Bulgaria we could rank here also the mountain massifs of Stará planina which have neither more marked mountain torrents, nor specific species combinations indicating that they would belong to East Carpathian variant.

Mediterranean zone

This zone has as a whole marked features following, on the one hand, from the water regime of the Mediterranean streams, on the other hand, from the development of this area lying in a periglacial Pleistocene territory. The pronounced geographical isolation of all three peninsulas of the Mediterranean Sea reflects itself also in the plecopterological communities. These peculiarities are the more striking, the more demonstrable this isolation is. That is why the Iberian associatons have more endemic species combinations than the Apennine and Balkan ones. The smallest differences are found in the currents, while the biggest ones in the mountain currents.

A. Lenitic currents

are similar to the Central European ones (with the exception of the thermophile variant). In respect of species they are very poor and their true original structure is not yet known. A considerable part of the currents is polluted as in Middle Europe and, therefore, without Plecoptera. The basic community is as. *Leuctra fusca — Xanthoperla apicalis*. Regionally we can divide it into four variants.

Var. Iberian with *Eoperla ochracea* (Fig. 25) has holo-European and Central-South European species. It is distributed mainly in the north and east of Spain in lowland streams.

Var. thermophile with *Tyrrhenoleuctra minuta* (Fig. 26) is restricted to the southwestern tip of the Pyrenean peninsula and is a very clearly defined variant which has an association in the system of communities. Involved are altogether endemic species, dependent on the periodic currents of this territory. Only an insignificant percentage is formed of species widely spread.

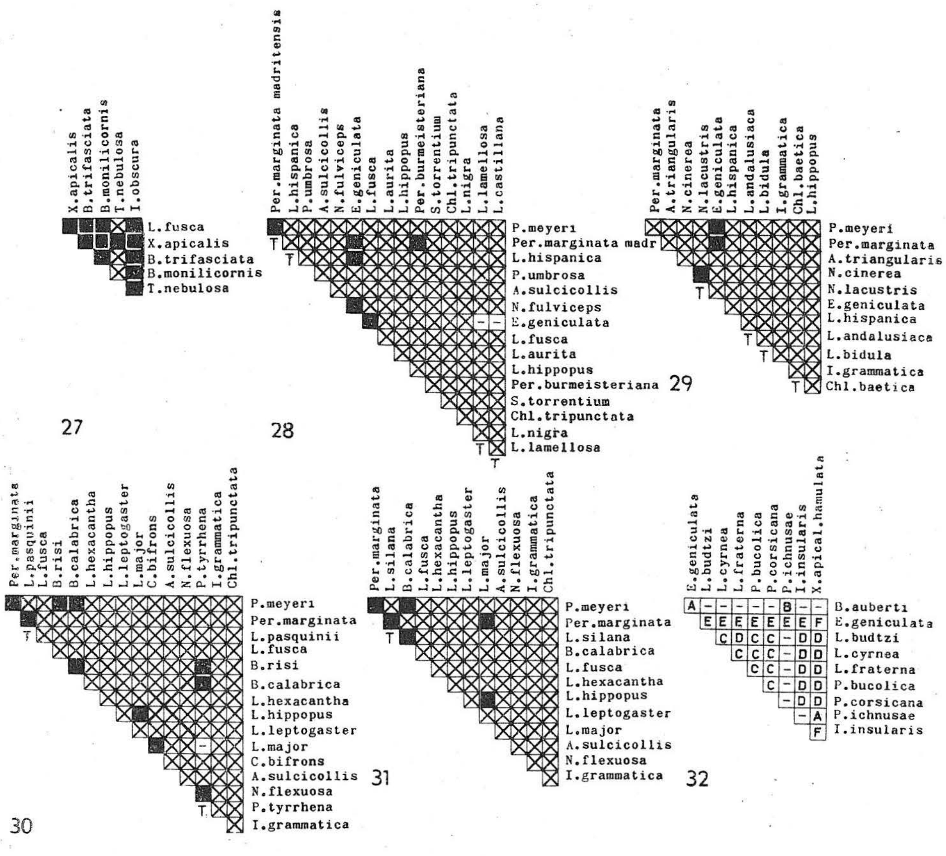
Var. Padua without *Eoperla ochracea* (Fig. 27) is developed in the Padua lowland of North Italy and has a Central European character. Its inclusion in the Mediterranean was performed for geographical reasons, because the northern Alpine barrier forms a marked water divide between Central and South Europe. In the community is missing *Brachyptera braueri.*

Var. Balkan with *Eoperla ochracea* is very little known to date. Aubert (1956, 1963) reports to have found in Grece only a few species, including circummediterranean *Eoperla ochracea.* Inasmuch this variant occurs, it is similar to the Paduan one. In the lenitic currents of the Adriatic coastal region, *Perla marginata* (lgt. Author) was also found. The occurrence of *Brachyptera trifasciata* and *Br. monilicornis* is little probable here.

B. Hilly-land and piedmont currents

These streams occupy the largest area in the Mediterranean in general. Compared with as. *Protonemura umbrosa — Perlodes microcephala* are poorer in species, but richer in endemic species combinations which distinguishes them from the others. The basic as. *Protonemura meyeri — Perla marginata* totals seven variants, whose stock is again formed of the widespread species. The fundamental structure is constituted again of the Central European and Central-South European species. Their distribution corresponds to the geographical zonality: each peninsula has two variants besides the insular one in the Tyrrhenian Sea.

Var. North Spanish with *Leuctra hispanica* [Fig. 28] comprises, on the other hand, species [*Leuctra hispanica, L. lamellosa*]. The number of endemic species in the community is not as high as in the following variants. It is distributed in the north and the northwest of Spain.



Mediterranean zone. Lenitic currents. As. *Leuctra fusca — Xanthoperla apicalis.* Fig. 27. Var. Padua without *Eoperla ochracea.* Hilly-land and piedmont currents. As. *Protonemura meyeri — Perla marginata.* Fig. 28. Var. North Spanish with *Leuctra hispanica.* Fig. 29. Var. South Spanish with *Leuctra andalusiaca.* Fig. 30. Var. Central Italian with *Leuctra pasquinii.* Fig. 31. Var. South Italian (Calabrian) with *Leuctra silana.* Fig. 32. Var. insular (tyrrhenian).

Explanations: Species combinations of A = Sardinian lenitic currents, B = Sardinian mountain currents, C = Corsican mountain currents, D = Corsican hilly-land currents, E = Sardinian and Corsican lenitic currents, F = Sardinian and Corsican hilly-land currents.

Var. South Spanish with *Leuctra andalusiaca* (Fig. 29) has more specific taxons than the preceding variant. It occupies the hilly-lands of Central and South Spain.

Var. Central Italian with *Leuctra pasquinii* (Fig. 30) resembles by certain species (*Nemoura flexuosa*) the Central German and Alpine ones (*L. hexacantha*), but differs from the others by the differential species (*Protonemura tyrrhena*). Compared with the two preceding variants, it does not feature a high number of endemic species.

Var. South Italian (Calabrian) with *Leuctra silana* (Fig. 31) is, on the whole, inconspicuous and resembles the preceding one. It has a number of species common with the preceding variant (*Brachyptera calabrica*), others are missing in this community (*Protonemura tyrrhena*). The principal habitat of this variant is Calabria, even though it is generally very poor in species.

Var. insular (tyrrhenian) — (Fig. 32) has all the features of insular isolation. Besides the species *Euleuctra geniculata,* the others are insular endemic species, common either to both islands (Corsica, Sardinia: *Isoperla insularis*), or actually only one of them (Corsica: *Protonemura corsicana;* Sardinia: *Protonemura ichnusae*). The insular variant misses wide-spread species, so that its classing with as. *Protonemura meyeri — Perla marginata* can be motivated only regionally and reconstructionally (generic post-Pleistocene species). With good reasons this variant might be denoted as association.

Var. Dinarian with *Dictyogenus imhofii* (Fig. 33) is little known to date. In the north of the Dinaric Alps, alpine species (*Rhabdiopteryx alpina, Siphonoperla montana*) mix with it, while in the south East Mediterranean species (*Protonemura albanica*). The actual Balkan species are few in number (*Brachyptera tristis*). This variant depends on karst, nonperiodic streams (Krka, Neretva).

Var. Thracian-Rhodopian with *Isoperla bureši* (Fig. 34) occurs in the east of Vardar in the Thracian-Rhodopian massif. Some species are common with the East Carpathian variant of the temperate zone (*Leuctra hirsuta, Isoperla belai*), while others are differential species of this variant (*Brachyptera thracica, Isoperla balcanica*). The stock is again formed of species widely distributed in Central and South Europe.

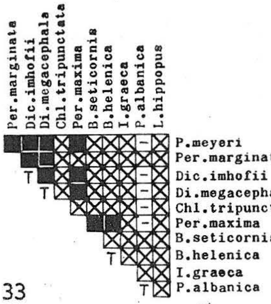
C. Mountain currents

These streams are not richer in species, but have the most characteristic communities. As a result of the action of geohistorical factors they are evolutionarily young species characterizing markedly every variant. The basis of the communities of mountain currents is formed of as. *Leuctra inermis — Perlodes microcephala* featuring a basic species composition very close to the Central European community. It is distributed in the mountainous regions of the Mediterranean and has a total of seven variants with numerous endemic species, of which only some with a high representation form differential species.

Var. Pyreneic-Cantabrian with *Protonemura spinulosa* (Fig. 35) occupies the mountain regions of North Spain, including the Pyrenees. In essence, two units can be distinguished: Pyreneic and Cantabrian, differing by specific, mostly alpine species. From the all-European point of view, the differentiation of both units is not so pronounced as to be able to speak in our sense of separate variants. The composition of the community features a smaller portion of species with a wide distribution (*Leuctra rauseri*) than the representation of endemic species.

Var. Central Spanish with *Protonemura navacerrada* (Fig. 36) has a marked preponderance of endemic species and geographical races. Involved is a Central Spanish, evolutionarily young variant stemming from the zone of the Tertiary Cordillera.

Var. South Spanish with *Brachyptera mussardi* (Fig. 37) is poor in species, even though specifically conspicuous. It is confined to the South Spanish Sierras (Sierra Nevada, Sierra Ronda) with specific conditions



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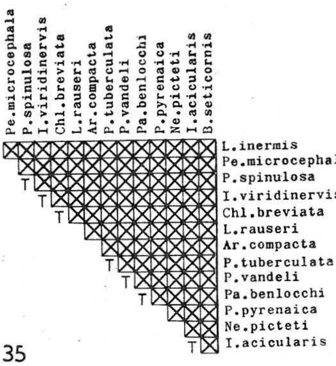

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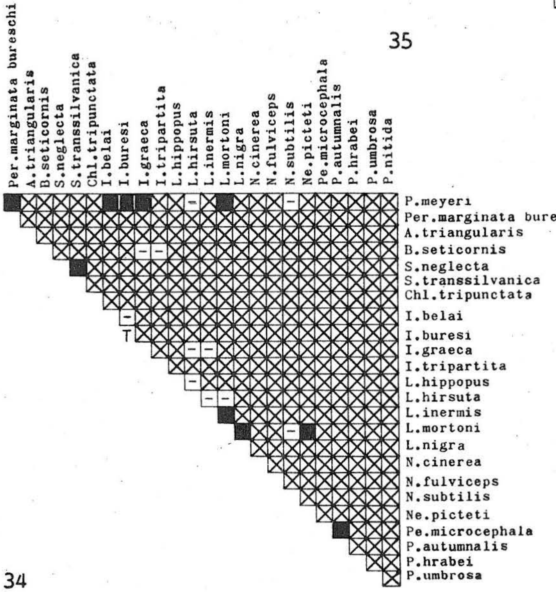

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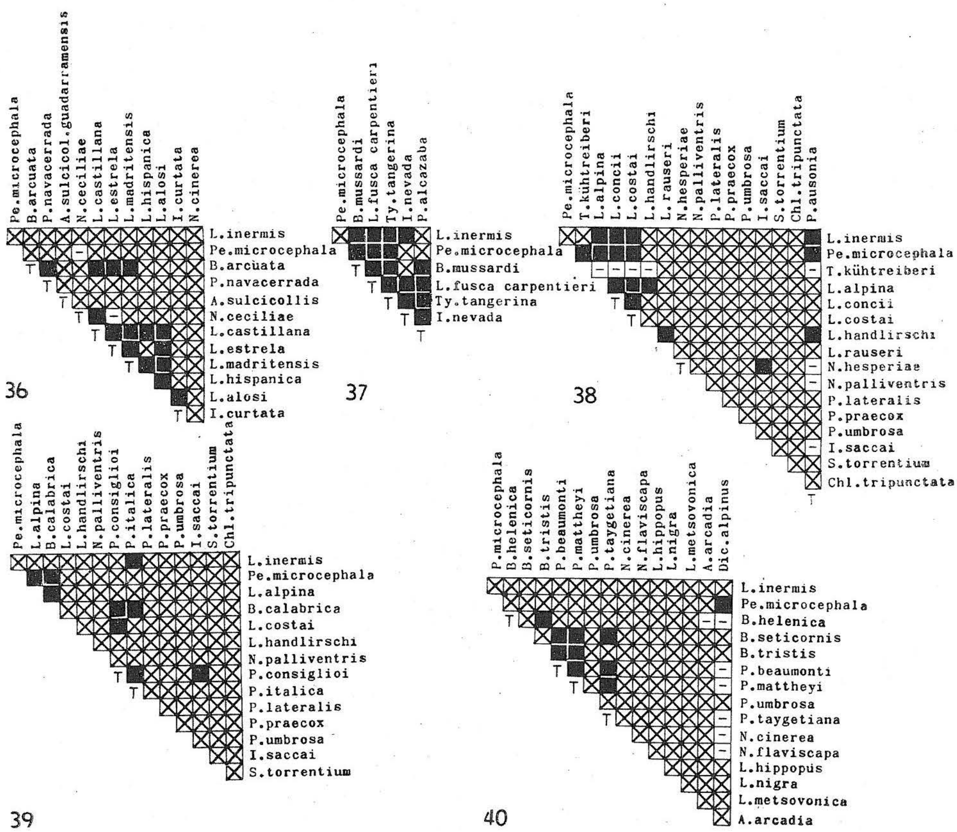
Mediterranean zone. Hilly-land and piedmont currents. As. *Protonemura meyeri — Perla marginata.* Fig. 33. Var. Dinarian with *Dictyogenus imhofii.* Fig. 34. Var. Thracian-Rhodopian with *Isoperla bureši.* Mountain currents. As. *Leuctra inermis — Perlodes microcephala.* Fig. 35. Var. Pyreneic — Cantabrian with *Protonemura spinulosa.*

of the environment (Aubert 1963). Some types of this variant occur also in North Africa.

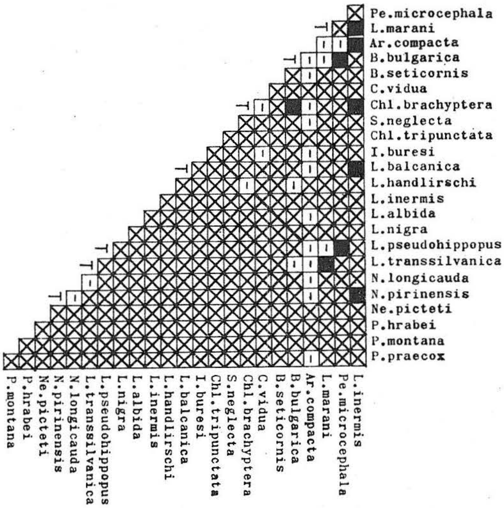
Var. Apenninian with *Protonemura ausonia* (Fig. 38) differs from the two preceding ones by a higher share of Central European and Central-South European species. Their distribution follows from the communication of the Apennines with the Alps in the north. That is why they also occur in species combinations with alpine species (*Leuctra alpina*).

Var. Silanian with *Protonemura italica* (Fig. 39) resembles the preceding ones. Next to the Apenninian species, progressive alpine species (*Leuctra alpina*) are also present here. Among the endemic species, the differential species of the genus *Protonemura* (*P. consiglioi, P. italica*) are striking.



Mediterranean zone. M o u n t a i n c u r r e n t s. As. *Leuctra inermis — Perlodes microcephala.* Fig. 36. Central Spanish with *Protonemura navacerrada.* Fig. 37. Var. South Spanish with *Brachyptera mussardi.* Fig. 38. Var. Apenninian with *Protonemura ausonia.* Fig. 39. Var. Silanian with *Protonemura italica.* Fig. 40. Var. Greek with *Protonemura mattheyi.*

Var. Greek with *Protonemura mattheyi* (Fig. 40) comprises a whole number of specific differential species (*Brachyptera beali, Protonemura beaumonti, Protonemura taygetiana, Leuctra metsovonica,* etc.) in addition to species widely distributed (*Leuctra hippopus, L. inermis, Brachyptera seticornis,* etc.). Some species (*Amphinemura arcadia*) are distributed also in the Rhodopian variant.



Mediterranean zone. M o u n t a i n c u r r e n t s. As. *Leuctra inermis — Perlodes microcephala.* Fig. 41. Var. Rhodopian with *Leuctra mařani.*

Var. Rhodopian with *Leuctra mařani* (Fig. 41) has a high share of both Central European and Central-South European species. Besides them, also species with a disjunctive area (*Protonemura montana*), Hercynian species (*Arcynopteryx compacta*), and Carpathian (*Isoperla bureši*) play a major role. They are distributed in the Thracian-Rhodopian massif. Among the differential species (*Leuctra mařani, L. balcanica*) there are some, confined to the individual mountain ranges (Vitosha: *Brachyptera bulgarica*).

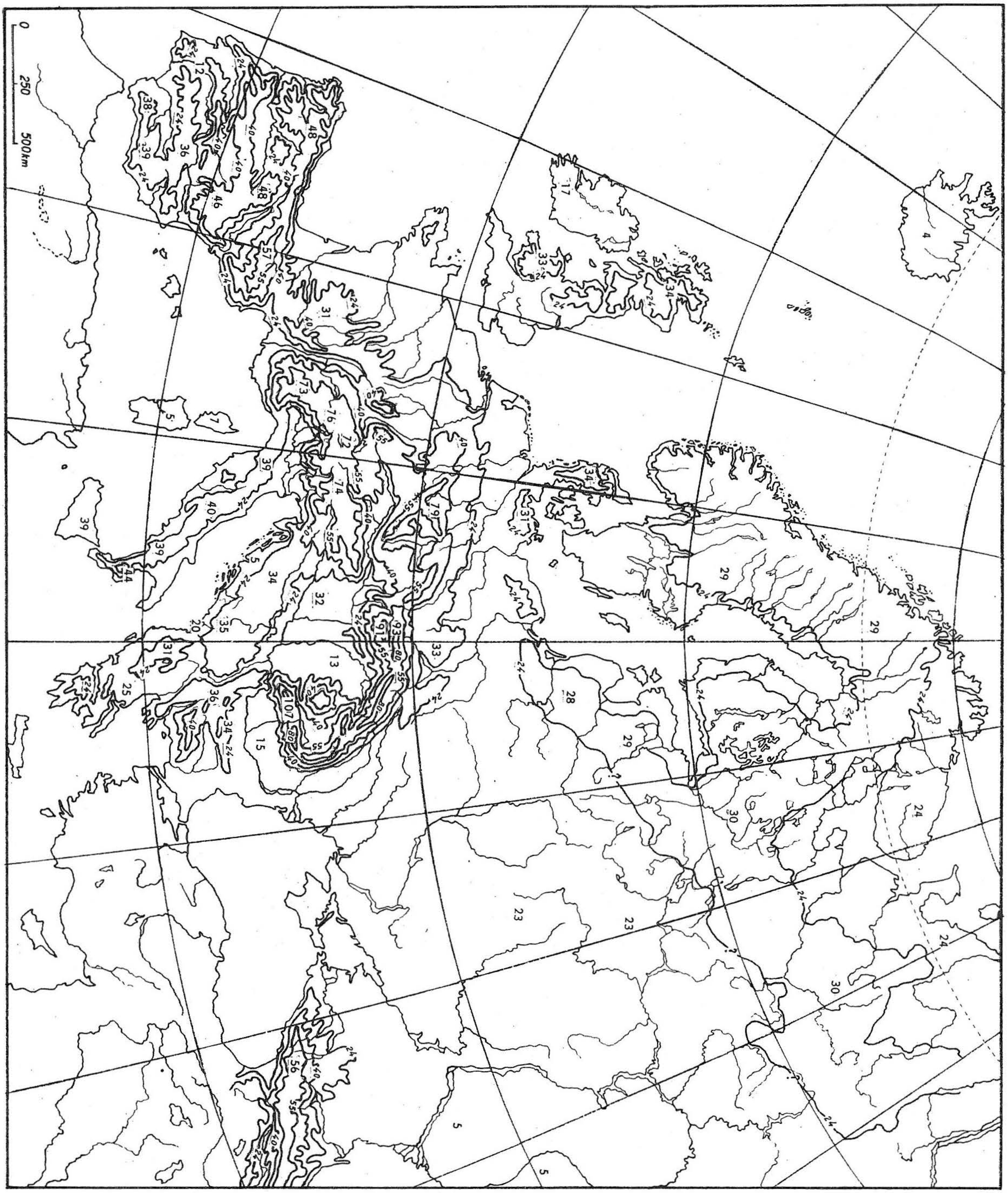


Fig. 42. Map of the isospecies of European Plecoptera. Explanations: The numbers state how many species live in the regions.
The lines separate the zones with 0—24, 25—40, 41—55, 56—80, 81 and more species.

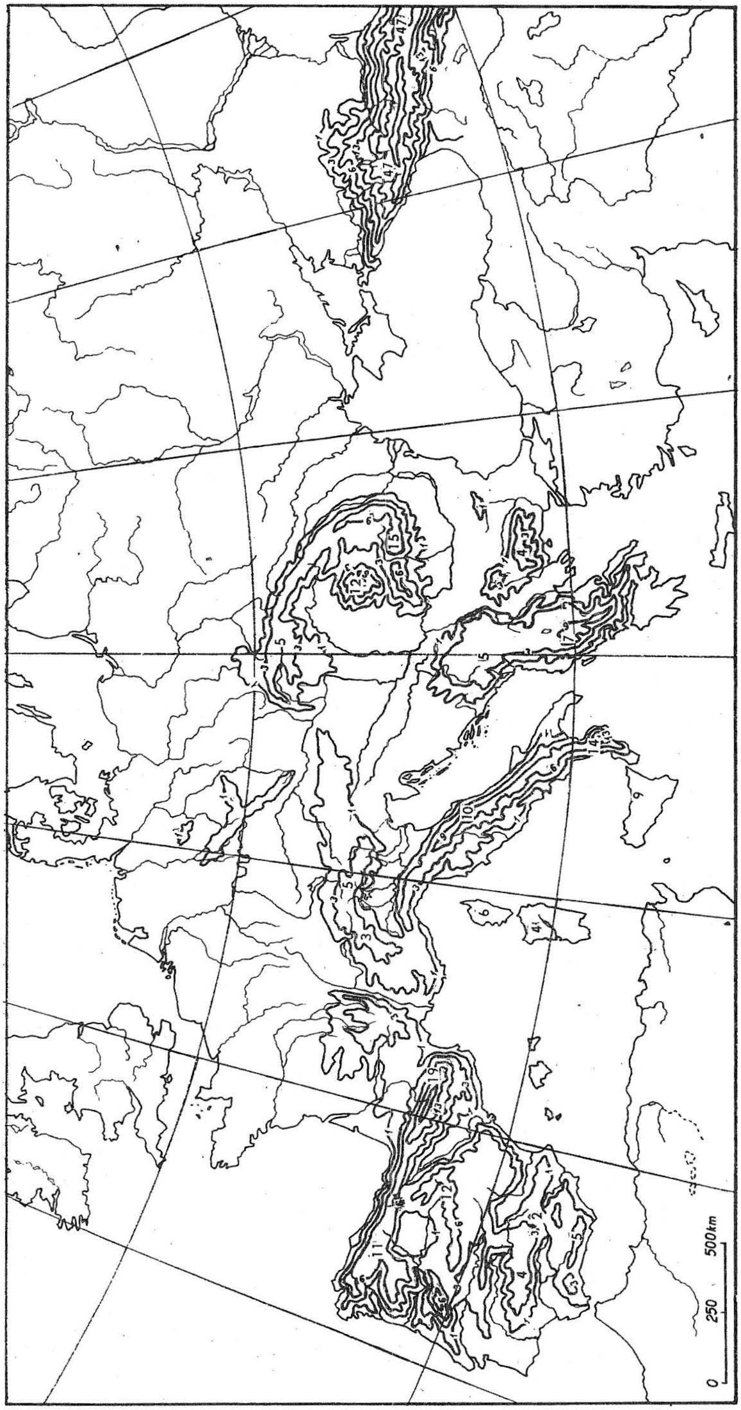


Fig. 43. Map of the isospecies of the European endemits. Explanations: The numbers state how many endemits live in the regions.
The lines separate the zones with 1—2, 2—5, 6—12, 13—20, 20 and more species.

II Evolution of Plecopterological Associations in Europe

The present picture of Plecoptera communities is the result of a long geohistorical evolution through which this important component of the bottom fauna of running waters has gone through in close association with its environment. From their present distribution it follows that the largest number of species is concentrated in the Central European region, their maximum being in the Eastern Carpathians. The lowest number of species is found in the lowland communities of lenitic currents. The Mediterranean area features approximately the same number of species as communities in the Pleistocene glaciation of North Europe. From the map of isospecies of Plecoptera (Fig. 42) thus follows that the highest number of taxons, irrespective of their genesis or chorological classification, is found in the mountainous regions.

The situation is different with isospecies of endemites (Fig. 43) which in associations and individual species play the role of differential species. Their maximum is concentrated in the Caucasus, while in respect of subspecies in the Pyrenees. A considerable number of endemic species is also found in the Eastern Carpathians. Northern and insular (Great Britain) Western Europe is without endemic species. Already earlier (Raušer 1962) I tried to demonstrate what constructive and destructive functions the Pleistocene fulfilled in the species composition of Plecoptera. Also the structure of Plecoptera communities (Fig. 44) is a reflex of these relations. The bulk of endemic species of South and Central Europe is made up of evolutionarily very young species, stemming from Würm and Riss. Some species are passing over today via geographical races to the formation of new species. Let us, therefore, compare the following table, compiled for the regions, established by Illies (1967) for "Limnofauna Europaea".

Number of region	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1*	44	38	41	69	33	24	33	74	83	92	28	11	32	39
2	27	19	33	19	2	11	10	5	2	21	—	1	1	—
3	12	3	6	4	7	6	8	10	15	17	14	11	14	15

Number of region	15	16	17	18	19	20	21	22	23	24	25
1	28	23	17	32	4	26	24	29	29	14	2
2	—	—	—	—	—	—	1	—	1	42	—
3	14	10	3	6	—	7	6	10	10	3	3

The essential differences in the number of species of whatever distribution and of the number of endemic species follow from their geographical evolution. It is beyond dispute that the species as fundamental elements of the living component of the community participate also in the development of the entire picture of the benthonic fauna of running waters.

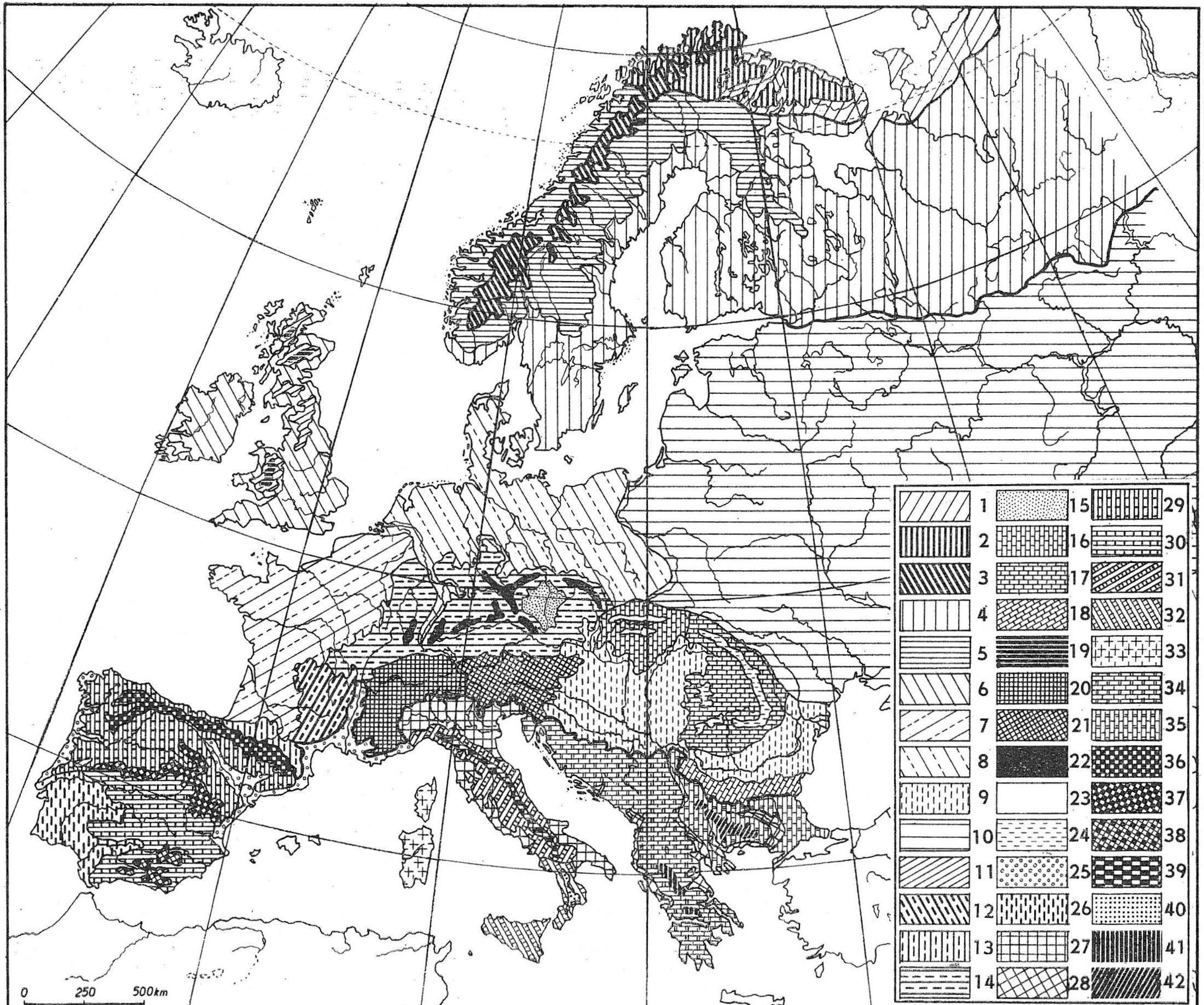
Let us compare now the individual associations of lenitic, hilly-land and piedmont, and mountain currents. In lenitic currents we do not en-

*) 1=number of species occurring *certainly* in the region at least in one, but, as a rule, in more places; 2=species occurring exclusively in this region and therefore are endemic species (as a rule in mountainous areas); 3=species occurring only or predominantly in lowland communities.

counter, with the exception of the Mediterranean region — any essential differences. Also the combination of true species is the same almost throughout Europe. This means that evolutionarily the associations of European lowland streams are of the same composition and, therefore, of the same age in evolutionary respect as well. Things are different with associations of hilly-land and piedmont currents. A differing community is typical of the arctic zone, another one again for the Mediterranean region. Analogous and very similar in composition are the communities of the boreal and temperate zones. They differ from one another only by the chorology of species that did not penetrate to the north beyond the boundary of maximum continental glaciation. The most striking differences in all four zones are displayed by the communities of the mountain currents. In the arctic zone, arctic species are present, in the temperate and Mediterranean zones with endemic species representing differential species of the individual variants occur. At the same time, the number of endemic species grows in the southern direction. In all the hitherto found communities (with the exception of the thermophile variant of lenitic currents) the frequently significant portion of widely distributed species is striking.

Already earlier I tried to show (Raušer 1962) what role is played by eurythermia and stenothermia of species and what share goes to the cold Pleistocene period in the formation of new species. Some years ago Illies (1952) demonstrated in the genus *Isoperla* Banks that the temperature conditions in the longitudinal section of currents play a significant role in the evolution of species of this genus. This "principle of Illies" has been verified not only in Plecoptera, but also in the other insect orders of the benthonic fauna and thus is becoming a generally valid evolutionary law. In this way the genesis of European Plecoptera communities can also be explained.

The onset of the cold Pleistocene period in Europe meant an outstanding intervention into their structure. It can be assumed that the original warm stenothermic species of the lowland communities either died out in situ or receded to European refuge areas in South or Southwest Europe. These association components returned then again to Central Europe after the continental glacier had regressed and enriched here again the decimated communities of euryoecic species. To them belong, e.g. *Marthamea vitripennis, Isoptena serricornis,* and others (Ost-West-Arten according to Illies 1953). In the unglaciated part of Europe those species could therefore maintain themselves which endure greater temperature variations, i.e. especially eurythermic species. This was the case in Central Europe. In that period we can also assume the communities of the lowland streams in South Europe to have been richer than the present ones, because there were far more favourable conditions of the type of forest climate. Proof of this is furnished, among others, also by the Iberian variant of lenitic currents where, besides Central European species, Mediterranean taxons (*Eoperla ochracea*) are typical. For hilly-land, piedmont, and mainly mountain currents the Pleistocene meant a significant enrichment of communities by evolutionarily younger species. Here it was first and foremost Illies' principle of climatic differentiation that



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came into play. The specific climatic and geomorphological conditions in the individual mountains were responsible that also a regional differentiation of communities on the level of variants occurred as well. In this way a rich distribution into groups of the Mediterranean association of mountain currents and the distinction of the variants of the Variscan and Alpine orogenies in Central Europe occurred. In the individual variants a further evolution followed manifesting itself in the distribution of variants into smaller units.

In a different way proceeded the evolution of the communities of Scandinavia. Their present picture is the result of the action of the continental glacier which destroyed the original rich communities. In their present day structure, euryoecic species penetrating to the north during its regression stage are abundant. A special component is formed of the arctic communities, among which the hilly-land and mountain currents exhibit a whole number of specific species [*Diura nanseni*] which otherwise do not occur in Europe of today. We, therefore, hold the view that they might either survive the unfavourable period on nunataks, or move from the unglaciated areas of North Russia [cf. Brinck 1949 : 227]. The arctic associations of the streams of this type might be a certain parallel to the Mediterranean associations for their specificity.

As the youngest members of communities we regard those species which penetrated from the East [Ost-West-Arten according to Illies 1953] and which today, first and foremost, are subject to human interventions in polluted streams [*Isoptena serricornis* in Holland according to Geiskes 1940 finally 1889].

The hitherto little differentiated communities of piedmont and mountain currents of certain orographic units furnish proof that the evolution processes beginning in the Pleistocene and continuing in the Holocene have not yet ended. These conclusions agree also with the conclusion of geomorphologists on the hitherto unbalanced gradient curve of currents and also with the research results of zoologists and botanists about geographical races as species in the status nascendi.

Fig. 44. Map of the plecopterological associations of Europe.

Explanations: Arctic zone. 1 = lenitic currents, 2 = hilly-land and piedmont currents, 3 = mountain currents and lakes.

Boreal zone. 4 = lenitic currents, 5 = hilly-land and piedmont currents.

Temperate zone. Lenitic currents. 6 = insular var. [=variant], 7 = West european var., 8 = Central German var., 9 = Pannonian var., 10 = Eastern var. Hilly-land and piedmont currents. 11 = insular var., 12 = Central Massif var., 13 = Subpyreneean var., 14 = Central European var., 15 = Bohemian var., 16 = Slovakian var., 17 = Transylvanian var., 18 = Stará planina var. Mountain currents. 19 = British var., 20 = West Alpine var., 21 = East Alpine var., 22 = Hercynian var., 23 = West Carpathian var., 24 = East Carpathian var.

Mediterranean zone. Lenitic currents. 25 = Iberian var., 26 = thermophile var., 27 = Balkan var. Hilly-land and piedmont currents. 29 = North Spanish var., 30 = South Spanish var., 31 = Central Italian var., 32 = South Italian var., 33 = insular var., 34 = Dinarian var., 35 = Thracian-Rhodopian var. Mountain currents. 36 = Pyreneic — Cantabrian var., 37 = Central Spanish var., 38 = South Spanish var., 39 = Apeninnian var., 40 = Silanian var., 41 = Greek var., 42 = Rhodopian var.

Finally, it is necessary to point to the interesting fact that just in Central Europe (cf. Illies 1955) there is a high number of Plecoptera species even though the portion of endemic species is low in general. It is also necessary to realize that Plecoptera as an amphibian component of the benthonic fauna have gone in Europe through a long terrestrial evolution. Their evolution is thus confined to those parts of Europe where there existed territories (asylums in the sense of Arldt 1919) that as islands played an important role in the evolution of the biota. Thus, parts of the Bohemian Massif (Šumava, Giant Mts), for example, have not been flooded by the sea since the early Carboniferous just as the Central French Massif. With the progressive paleogeographical changes the surface of dry land also increased in Central Europe. That was the case in the German Highland and in the Alps. The Alpine orogenesis influenced in the Tertiary the character of the communities in a striking manner. The older Hercynian species were joined by younger Tertiary mountain forms. It is of interest to note that the Carboniferous glacial period in southern and the Pleistocene one in the northern hemisphere are a condition for the heterogenity of present Plecoptera. Rich finds of Protoperlaria and Archean Plecoptera in the Permian and the Triassic and the present occurrence of Plecoptera are their result. We thus can say that the positive influence of the cold Pleistocene manifests itself in the very species wealth of Central Europe.

The population dynamics in the individual species furnish proof that really a dying-out, evolutionarily archaic insect group is concerned, whose present distribution and composition of communities is a reflex of the long gone-by past. It therefore deserves our attention and protection.

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